

doing excellent research. I would just hope that some of them would get more support.

#### **How has the environment at the Champalimaud Neuroscience Programme influenced your work?**

We develop and use high resolution, dynamic, quantitative readouts of behavior. This is a real strength at the institute and strongly resonates with me due to the approach I developed while working on the cell biology of trachea morphogenesis. For me, biology is about regulating dynamic processes and if you really want to understand what is going on you need to get a handle on the dynamics of the system. In cell biology, modern microscopy gave the field access to a rich understanding of the behavior of cells. In behavior we often use a bar graph to describe the complex behavior of the animal. There is no way we will understand behavior if we stick to that level of description. And I am not talking about getting rid of reductionism; I would call it 'enriched reductionism'. This type of approach is common to many groups at the CNP, and we would not have pushed that aspect of our work as much somewhere else.

**What is your favorite scientific meeting?** Definitely the JEDI meeting — not a Star Wars convention, JEDI stands for Junior European *Drosophila* Investigators and is a new, self-organized gathering of early career scientists working on *Drosophila* in Europe and having recently established their independent research group. We meet once a year somewhere in Europe to discuss our science and exchange our experiences in establishing our independent research programs. The science is always excellent, the extremely informal setting fosters interactions and the parties are great. So you get both a great peer support group to help you with the challenges of being an independent young group leader and a great scientific network to establish collaborations.

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## Quick guide

### Peacock spiders

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**What is a peacock spider?** Peacock spiders are small (2–6 mm) jumping spiders belonging to the genus *Maratus*, a group endemic to Australia. Males generally have conspicuously colorful abdomens as well as elongated third legs that are brown/black and often tipped with white brushes (Figure 1). By contrast, females are cryptically colored, usually mottled brown/beige. During courtship, a male peacock spider will raise his abdomen, and wave it at a female in synchrony with his third pair of legs. Males of many species also have lateral flaps that can be extended from their abdomen like a fan; this fan-structure, together with remarkable ornamentation of *Maratus* males, is reminiscent of a peacock's display, hence their common name.

Jumping spiders make up the largest family (Salticidae) in the order Araneae, and based on the rich array of morphology, behavior and ecology of the group, salticid diversity rivals that of birds. *Maratus* spiders are part of the salticid subfamily Euophryinae, and while euophryine monophyly is well supported, distinguishing between *Maratus* and closely related genera is difficult (J. Waldo, personal communication). Within *Maratus*, relationships between species are currently not well understood, but evidence suggests there are upwards of 40 species, and perhaps many more yet to be discovered. At present, several morphological and behavioral species-groups are evident (M.G., personal observation) and ongoing molecular work will eventually determine the validity of these groupings.

#### **When and where are they found?**

Peacock spiders are most active during their breeding season, the Austral Spring. Mature males emerge as early as August and persist in large numbers until December. Mature females typically appear a little later and survive longer than males, although they too become

scarce by December, when they tuck themselves away to lay and guard egg sacs. While these patterns generally hold, in actuality, male and female activity is highly variable during this period, seemingly species and region specific.

Peacock spiders are widespread across the southern-half of Australia and live in a diverse range of habitats, from sand dunes on the temperate coasts to grasslands in the semi-arid regions (J. Waldo, personal communication). As is true for many salticids, some *Maratus* species, such as *M. volans*, have a large distribution and occupy a wide array of environments. On the other hand, several peacock spiders are more specialized or geographically limited; for example, *M. sarahae* is found exclusively in heath habitats on two peaks in the Stirling Ranges. The majority of peacock spiders studied are ground-dwelling, predominantly found on leaf-litter under eucalypt woodlands. However, some species, such as *M. speciosus*, seem to occur more in shrubs or young grass-trees (*Xanthorrhoea*).

**What do they eat, and how do they hunt?** Peacock spiders are diurnal cursorial hunters feeding primarily on insects and other spiders. The evolution of an acute visual system in salticids almost certainly originated as an adaptation for stalking prey. However, this development also facilitated a wandering lifestyle different from that of their sit-and-wait ancestors, enabling jumping spiders to roam and encounter many environments. Keen eyesight has probably been useful for peacock spiders in navigating, inhabiting and exploiting new types of habitats, and undoubtedly set the stage for the evolution of complex visual signals.

#### **How do males produce their visual signals?**

Tiny scales/hairs produce the distinct color patterns observed across the group. Like many other salticids studied to date, peacock spider scales reflect light in both the visible and/or ultraviolet range (M.G., unpublished data). Multilayer reflectors are responsible for producing the iridescent colors seen in several salticids. While only a few peacock spider species have been examined in any detail, it appears that blue and green iridescent scales

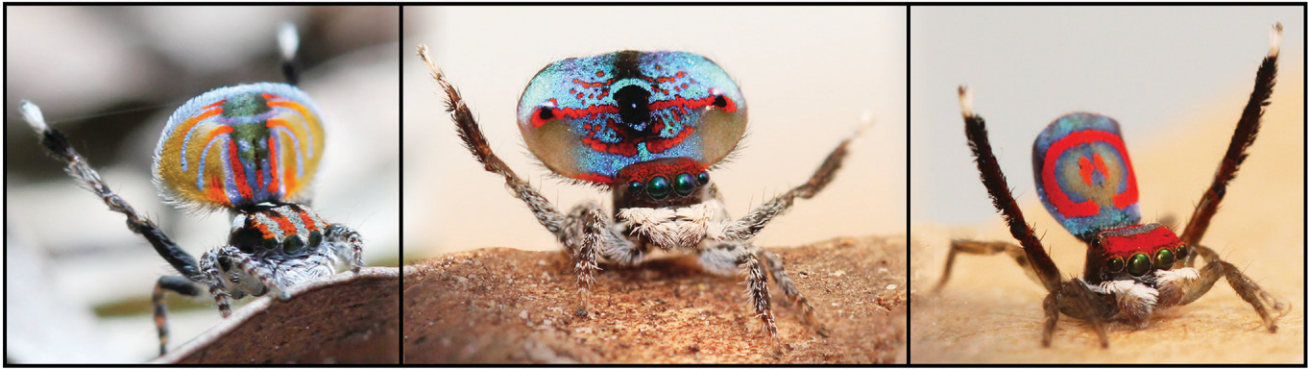


Figure 1. Courtship displays of three different male peacock spider species. From left to right, *M. volans*, *M. mungiaich* and *M. splendens*.

of *Maratus* males combine surface diffraction gratings with multilayer reflectors to produce interference-based colors. In contrast to this 'structural color', the red and yellow patches of *Maratus* males instead arise from pigmented brush-like hairs.

*Maratus* males are among the most brightly colored and sexually dimorphic of the salticids. Fortunately, the detection and processing of such amazing colors isn't a problem for jumping spiders, which are among the most visually advanced of the invertebrates.

#### How is their visual system special?

Using the full complement of eyes (eight), jumping spiders have exceptional abilities to perceive motion and depth. Furthermore, specialized structures in their primary eyes have allowed them to approach the physical limit of optical resolution for their compact size. Their minimum resolution angle (acuity) is about  $0.04^\circ$ , or about  $1/13$  the diameter of the sun disk; this is not much worse than ours ( $0.007^\circ$ ) and considerably better than the best insects ( $0.4^\circ$ ).

Salticids are easily distinguished from other spiders by their enlarged anterior median eyes. These eyes are equipped with a telephoto lens and a tiered retina, each layer containing photoreceptor cells of distinct absorption spectra. Salticid color vision is much better than ours, more similar to that of birds, with as many as four evenly spaced channels, including a UV-sensitive photoreceptor (humans have only three and no UV sensitivity). There is strong morphological and behavioral evidence for color vision being used in both predation and sexual selection. Not surprisingly, the region

of jumping spider brains used for visual processing is much larger than that of other comparably sized arthropods, and color learning has been demonstrated.

**Do peacock spiders use other signals?** Substrate-borne vibrations are important for mating success in several salticids, including at least one species of peacock spider, *M. volans* (M.G., unpublished data), and likely many more. *Maratus* males seem to use their abdomens almost exclusively to produce vibrations. A preliminary high-speed video analysis showed that the primary form of signal production is tremulation (M.G., unpublished data), simple vibrations originating from rapid movements of the abdomen. Some species also have a percussive signal that they will use intermittently throughout their display. Although males appear to be drumming their third legs on the ground, in fact, the majority of percussive energy is produced through abdominal contact with the substrate (M.G., unpublished data). A third signal production mechanism, stridulation, may be used occasionally, but seems less common in this group.

In addition to visual and vibratory signals, *Maratus* males may also make use of chemical communication to locate and secure a mate. Salticids do not build webs, but they constantly produce silk as they move about their environment. Contact pheromones in salticid silk drag-lines are common, and these are detected by chemoreceptors on both the legs and palps. While visual cues alone can elicit courtship in salticids, contact pheromones can also trigger male courtship in the absence of visual

cues; this has been directly observed with many species of peacock spiders (M.G., unpublished data). While there is less empirical evidence for salticids using airborne pheromones, they may also be important. As female peacock spiders are often very aggressive once they have already mated, it may be vital for males to identify a female's receptivity and quality from contact or airborne pheromones before risking getting close enough to court.

#### How does male courtship proceed?

Peacock spiders have elaborate courtship, even by salticid standards. During a search for a mate, a male will periodically pause atop a perch to wave his third pair of legs, presumably to attract the attention of any females nearby. When a male finally spots a female, he may begin courtship by producing vibrations. If the female orients towards the male, he will raise his abdomen, extend his abdominal fan-flaps and wave the whole structure back and forth, accompanied by third leg movements that accentuate this dance.

Male courtship ranges from a few minutes to over an hour, depending on the female response. If a male is not attacked nor does the female flee, he will slowly approach her, dancing and vibrating as he does so. When he is a distance of about one body length from the female, he commences what is known as the pre-mount display, a highly conserved behavior across the genus. This display lasts until the male completes his advance and attempts to mount and mate with the female. As with courtship, copulation duration can range from several minutes to an hour or more (M.G., unpublished data).

Mating trials conducted with *M. volans* indicate that *Maratus* females are very choosy, and once a female has already mated, she is unlikely to mate again (M.G., unpublished data). Compared to virgins, mated females are also more aggressive and generally spent a lower proportion of time attending subsequent males' displays (M.G., unpublished data). Overall, low mating rates, and no multiple mating, suggests that strong sexual selection is operating in this system.

**Is there other evidence for sexual selection in this group?** Male sexually selected traits and visually mediated displays are important during courtship of females in the majority of salticids examined. The complex display repertoires of jumping spiders probably reflect sexual selection rather than a need for reproductive isolation or reduction of cannibalism. In peacock spiders, and other salticids using abdominal displays, the location of abdominal ornaments correspond to how and from what direction the abdomen is held and waved so that the female can see the ornaments during courtship.

Peacock spider males do not develop their bright colors until they become mature, further suggesting a strong role for sexual selection in generating conspicuous male appearances. Moreover, there is direct genetic and behavioral evidence for sexual selection in jumping spiders. Numerous studies across the family show an association between species richness and the development of sexual traits, suggesting that sexual selection, supported by superb vision as a key innovation, could be an important driver of diversity in the group.

**Why are peacock spiders a unique biological system?** Small terrestrial arthropods are inherently different from their well-known vertebrate counterparts: because of this large phylogenetic gap, these organisms provide exceptional opportunities to test our understanding of fundamental biological principles. For example, are there processes that are unique to the miniature spatial scales on which salticids operate? Also, what is the cognitive architecture required for organisms of such a compact size to produce, perceive, and process

complex behavioral displays? Members of the *Maratus* genus exhibit some of the most spectacular arthropod displays known. Different species vary widely in habitat as well as visual and vibrational signaling traits, making them particularly tractable for studies of multi-modal signaling. While we are only just beginning to uncover aspects of their physiology, behavior, and ecology, it is clear that peacock spiders will enrich our understanding of sensory ecology, sexual selection, and trends in diversification.

#### Where can I find out more?

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## Primer

## Algae

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Algae frequently get a bad press. Pond slime is a problem in garden pools, algal blooms can produce toxins that incapacitate or kill animals and humans and even the term seaweed is pejorative — a weed being a plant growing in what humans consider to be the wrong place. Positive aspects of algae are generally less newsworthy — they are the basis of marine food webs, supporting fisheries and charismatic marine megafauna from albatrosses to whales, as well as consuming carbon dioxide and producing oxygen. Here we consider what algae are, their diversity in terms of evolutionary origin, size, shape and life cycles, and their role in the natural environment and in human affairs.

#### Defining algae

Algae are not readily defined. An alga can be broadly described as an organism carrying out oxygen-producing (oxygenic) photosynthesis that is not a 'higher plant' (embryophyte). **Figure 1A** indicates oxygenic photosynthesis in terms of chemical substrates and products, but not their stoichiometry. This definition includes cyanobacteria and eukaryotes in a number of clades with the eukaryotic algae originating from a symbiosis between a non-photosynthetic eukaryotic cell and a photosynthetic cyanobacterium. However, phylogenetic definitions of algae conflict with the 'oxygenic photosynthesis' part of the definition given above because there have been multiple losses of the capacity for photosynthesis. Such losses have also occurred in embryophytes, adding to the complexity of trying to define these lineages in functional terms. While oxygenic photosynthesis is monophyletic, the eukaryotic algae are polyphyletic. This is explained by the occurrence of serial endosymbioses. The primary endosymbiosis giving rise to eukaryotic algae involved the incorporation of a cyanobacterium by a eukaryote to produce the chloroplasts of a clade comprising glaucocystophytes, red and green algae (and hence